

# Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the white-breasted thrasher, *Ramphocinclus brachyurus*

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## Abstract

Dispersal is a fundamental process influencing evolution, social behaviour, and the long-term persistence of populations. We use both observational and genetic data to investigate dispersal, kin-clustering and intergroup relatedness in the white-breasted thrasher, *Ramphocinclus brachyurus*, a cooperatively breeding bird that is globally endangered. Mark-resighting data suggested sex-biased dispersal, with females dispersing over greater distances while males remained philopatric. Accordingly, spatial autocorrelation analysis showed highly significant fine-scale genetic structure among males, but not among females. This fine-scale genetic structuring of the male population resulted in very high levels of relatedness between dominant males at neighbouring nests, similar to that seen within cooperative groups in many species where kin selection is cited as a cause of cooperation. By implication, between-group as well as within-group cooperation may be important, potentially creating a feedback loop in which short-distance dispersal by males leads to the formation of male kin clusters that in turn facilitate nepotistic interactions and favour further local recruitment. The strength of spatial autocorrelation, as measured by the autocorrelation coefficient,  $r$ , was approximately two to three times greater than that reported in previous studies of animals. Relatively short dispersal distances by both males and females may have a negative impact on the white-breasted thrasher's ability to colonize new areas, and may influence the long-term persistence of isolated populations. This should be taken into account when designating protected areas or selecting sites for habitat restoration.

**Keywords:** cooperative breeding, kinship, mating system, microsatellites, *Ramphocinclus brachyurus*, white-breasted thrasher

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## Introduction

Dispersal is a life history trait that plays a fundamental role in population biology, behavioural ecology, and conservation (Koenig *et al.* 1996). It influences biological processes at almost every ecological level from the genesis and extinction of species (Mayr & Diamond 2001; de Siqueira *et al.* 2004), to the structure of communities (Dieckman *et al.* 1999), the dynamics and persistence of populations (Hanski 1998) and the social interactions between individuals (Clobert *et al.* 2001). However, remarkably little

is known about dispersal (Dieckman *et al.* 1999), largely because it is difficult to study. Measuring dispersal in the field typically requires intensive, long-term demographic studies (Koenig *et al.* 1996) and even when such detailed long-term data sets are available, dispersal distances are often systematically underestimated because of the restricted size of study areas (Barrowclough 1978; Rousset 2001).

Genetic studies provide an alternative, and potentially less labour-intensive, means of quantifying dispersal (Double *et al.* 2005). Genetic studies of dispersal have traditionally adopted a classic model of population structure, viewing a species' distribution as a set of semidiscrete subpopulations, each composed of males and females

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mating at random (Wright 1969, 1978). This model enables interpopulation measures of gene flow and migration (such as Wright's *F*-statistics) to be made, but does not facilitate the measurement of dispersal at a fine scale, i.e. within subpopulations (Manel *et al.* 2003; Double *et al.* 2005). A further limitation of these traditional measures of gene flow and dispersal between subpopulations is that they reflect evolutionary averages rather than contemporary patterns of dispersal (Bossart & Prowell 1998; Palsboll 1999).

More recently, a suite of new techniques has been developed to describe contemporary genetic dispersal using hypervariable molecular markers such as microsatellites in conjunction with both existing and novel statistical procedures (Manel *et al.* 2003). These new techniques include spatial autocorrelation analysis which enable detection of whether or not the genetic similarity between neighbouring individuals is greater than that expected by chance. Modern autocorrelation procedures offer randomization procedures for statistically testing the null hypothesis of no spatial genetic structure.

A key advantage of these techniques is that they are individual- rather than population-based, and are thus of particular use in investigating within-population dispersal when there are no clear a priori means of delimiting population boundaries. Although spatial autocorrelation analysis was pioneered in the 1970s (Sokal & Neal 1978), it is only in more recent years that the traditional allele-by-allele and locus-by-locus approach has been replaced by more powerful multivariate methods that minimize stochastic noise (Smouse & Peakall 1999).

Many animal species exhibit natal philopatry, restricted dispersal and complex social organization (Wilson 1975; Greenwood 1980; Greenwood & Harvey 1982), characteristics that might be expected to generate significant fine-scale non-random genetic patterns that could be detected using spatial autocorrelation. However, although widely used in the study of plants (e.g. Epperson & Li 1996; Epperson & Alvarez-Buylla 1997; Sokal *et al.* 1997; Smouse & Peakall 1999), spatial autocorrelation analysis rarely has been employed to investigate spatial genetic structure in animal populations (e.g. Peakall *et al.* 2003) and we could only find one published study of a bird that used this method (Double *et al.* 2005). Indeed, it seems generally true that fine-scale genetic structuring has received less attention in birds than in many other groups (Double *et al.* 2005). This may reflect an assumption that dispersal patterns and genealogical lineages inferred from long-term banding studies provide a reliable indication of fine-scale spatial genetic structure. However, it has become increasingly clear that it is not always safe to infer genetic relationships from behavioural observations (Koenig & Dickinson 2004).

We used a recently developed multivariate and multi-locus form of spatial autocorrelation analysis (Smouse &

Peakall 1999) to investigate fine-scale genetic structure and kin clustering in the white-breasted thrasher, *Ramphocinclus brachyurus*, a cooperatively breeding bird. Spatial autocorrelation analyses are typically used to infer biological processes (i.e. dispersal, mating system, social behaviour) based on fine-scale genetic patterns when demographic data are lacking (Double *et al.* 2005). However, our study is part of a 3-year investigation of white-breasted thrasher social behaviour (Temple 2005), and so we were able to compare spatial genetic patterns with information on dispersal, mating system and group structure derived from long-term observation. White-breasted thrashers are highly sedentary and live year-round in small family groups, with offspring both sexes remaining philopatric at least in their first year (Temple *et al.* in review), suggesting high potential for fine-scale genetic structure to develop.

Knowledge of spatial genetic structure in this species potentially has practical as well as theoretical applications. Spatial autocorrelation analysis can provide insights into processes such as immigration, emigration, and the dynamics of source and sink populations that are of use in the conservation management of threatened species (Cassens *et al.* 2000). Understanding the spatial determinants of genetic structure enables conservationists to determine the proper spatial scale for management and demographic studies (Manel *et al.* 2003). The white-breasted thrasher is classified as 'Endangered' (BirdLife International 2000, 2004), and is at greater risk of extinction than any other avian cooperative breeder (Walters *et al.* 2004). We conclude by considering the relevance of our findings for the conservation management of this species.

## Materials and methods

### *Study site, study species and field methods*

White-breasted thrashers are medium-sized (52–66 g) cooperatively breeding passerines that inhabit dry woodland and scrub on the east coasts of St Lucia and Martinique (Lesser Antilles). Thrashers form territorial groups consisting of a dominant male and female, often assisted by up to three nonbreeding helpers. Both males and females act as helpers, in roughly equal proportions. Helpers are retained offspring from previous breeding attempts, and are almost invariably first-years; older birds disperse to breed independently (Temple *et al.* in review). Rates of extra-pair fertilization are fairly low, with 7.5% of chicks being fathered by extra-group males ( $n = 67$ ), and there is no unequivocal evidence of joint nesting (Temple *et al.* in review). Male helpers sometimes obtain territories by a 'budding' process, creating a new territory adjacent to (or incorporating part of) their natal territory, whereas female helpers have never been observed to acquire a territory in this fashion (Temple *et al.* in review).

**Table 1** Characteristics of the six microsatellite loci, including polymorphism characteristics, for the 253\* white-breasted thrashers genotyped during the 3-year study

Locus	Number of alleles	Size range (bp)	Observed heterozygosity
WB2	6	213–223	0.715
Th3	6	136–156	0.770
WB5	8	168–202	0.679
Th6	6	144–164	0.618
Th12	2	153–155	0.263
Th15	4	151–159	0.550
Overall	5.33	136–223	0.601

\*Although 261 thrashers were captured, only 253 were blood-sampled and genotyped.

The study site is a remnant of coastal scrub woodland on the east coast of St Lucia, between the settlements of Denery and Praslin (13°55'N, 60°55'W). This 680-ha fragment is home to roughly 1200 full-grown adults and yearlings, just over three-quarters of the global population of the white-breasted thrasher (Temple 2005). Over three seasons we caught and uniquely marked 100 adults and 119 chicks on 63 territories spread over one main study site and four smaller satellite sites, which together occupied a total area of 100 ha. A further 19 adults and 23 chicks were ringed at sites outside the core study area. Capture, marking, ageing, sexing and blood-sampling protocols are detailed in Temple *et al.* (in review). Breeding attempts were monitored and behavioural data were collected, as described in Temple *et al.* (in review), during three breeding seasons (April–June 2002, March–August 2003, April–September 2004). To quantify dispersal we searched for marked individuals throughout the 100-ha study area during the 2003 and 2004 breeding seasons. The whole 680-ha remnant of dry woodland was searched opportunistically in 2003 during a randomised habitat and population survey that covered the entire range of the thrasher on St Lucia (Temple 2005). The locations of resighted individuals were recorded using a handheld Garmin 12XL GPS receiver and imported into ARCVIEW GIS 3.1 (Geographic Information System by ESRI 1999). The distance dispersed by each individual was then measured on the projected aerial image. If the resighted juvenile had remained on its natal territory, the dispersal distance was recorded as zero.

#### Microsatellite genotyping

Six microsatellite loci developed specifically for white-breasted thrashers (Jin *et al.* 2006) were used for the spatial autocorrelation analysis and the calculation of relatedness between nearest neighbours (Table 1). Genotyping was carried out as described in Jin *et al.* (2006). In total, 253 birds

were successfully genotyped. Thirty-two different alleles were found in these 253 individuals, with a mean number of alleles per locus of 5.33 and an average observed heterozygosity of 0.601.

#### Spatial autocorrelation analyses

Autocorrelation analyses were carried out using genotypic data from the 98 adult white-breasted thrashers whose territory location and breeding status during the 2004 breeding season were known. Data from 50 different territories were used (see Fig. 1), with 44 dominant males (88% of the total number of dominant males present,  $n = 50$ ), 28 dominant females (56%,  $n = 50$ ), 13 male helpers (93%,  $n = 14$ ) and 13 female helpers (100%,  $n = 13$ ) being sampled.

We used spatial autocorrelation techniques developed by (Smouse & Peakall 1999; Peakall *et al.* 2003; Double *et al.* 2005) which employ a multivariate approach to assess simultaneously the spatial signal generated by multiple codominant microsatellite loci. All analyses were performed using GENALEX 6 (Peakall & Smouse 2006). This software calculates an autocorrelation coefficient  $r$  using two pairwise matrices, one containing geographic distances and the other containing squared genetic distances (following Smouse & Peakall 1999). The autocorrelation coefficient  $r$  is calculated for a specified number of distance classes, and provides a measure of the genetic similarity between pairs of individuals falling within each distance class.

Pairwise individual-by-individual genetic distances for the codominant microsatellite loci were calculated via the methods expounded by Peakall *et al.* (1995) and further explained in Smouse & Peakall (1999). In brief, for a single-locus analysis of a microsatellite marker with  $i$ th,  $j$ th,  $k$ th and  $l$ th different alleles, a set of squared distances is defined as  $d^2(ii, ii) = 0$ ,  $d^2(ij, ij) = 0$ ,  $d^2(ii, ij) = 1$ ,  $d^2(ij, ik) = 1$ ,  $d^2(ij, kl) = 2$ ,  $d^2(ii, jk) = 3$  and  $d^2(ii, jj) = 4$ . Individual matrices for each locus are summed across loci, under the assumption of statistical independence. This assumption is reasonable, since the six microsatellites employed showed no evidence of linkage disequilibrium (Temple *et al.* in review). The linear pairwise geographic distance matrix was calculated from the X- and Y-coordinates of the centre of each of the 50 territories at which birds were sampled (Fig. 1). Because territory boundaries were not mapped in this study, the territory centre is defined as the Euclidean centre point of all nests found on a territory. The average distance to the centre of the nearest neighbouring territory was 70.0 m ( $\pm$  SE 5.76,  $n = 50$ ). All individuals resident on the same territory were given identical coordinates. Variable distance classes were used, because there were distances of up to 2.45 km between sample pairs, but previous research suggested that spatial autocorrelation was likely



**Fig. 1** Distribution of the 50 territories at which 98 genotyped full-grown birds were known to be resident during the 2004 breeding season, on which the spatial autocorrelation analyses are based.

only to occur in the first few hundred metres (Double *et al.* 2005). The first boundary was set at 5 m, to ensure that this distance class contained only within-territory comparisons. Points 5–70 m apart were assigned to the 70-m distance class, points 70–140 m apart were assigned to the 140-m distance class, and so forth. From 70 to 700 m the class size was set at 70 m (one average territory width), from 700 to 1400 m the class size was 140 m (two territory widths), and from 1400 to 2450 m the class size was 350 m (five territory widths). Territories were distributed randomly (as opposed to regularly) across the study area (Fig. 1), resulting in a relatively even frequency distribution of interterritory distances. The same distance classes were used for all analyses.

Spatial genetic autocorrelograms were produced by plotting the calculated autocorrelation coefficient,  $r$ , as a function of distance. Tests for statistical significance were performed as described by Peakall *et al.* (2003). Two methods were used: random permutation and bootstrap estimates of  $r$ , with the number of permutations and bootstraps set to 1000. For small samples, bootstrap errors tend to be larger than permutational errors, and consequently bootstrap tests are more conservative and will favour the null hypothesis more frequently than permutational tests. Here, we report both the results of bootstrap

and permutational tests, but declare significance only when both tests indicate a significant result at  $P < 0.05$ .

#### *Estimation of relatedness*

Although autocorrelation coefficients such as  $r$  and Moran's  $I$  are closely correlated with estimates of relatedness (Banks *et al.* 2005), they do not provide a surrogate measure of genealogical relationships. In order to explore the implications of kin-clustering further within white-breasted thrasher populations it was valuable to calculate a direct estimate of relatedness between interacting neighbours. Relatedness ( $R$ ) is a continuous measure of overall identity by descent (IBD) between individuals (Blouin 2003), with IBD being the situation in which two alleles are descended from a common ancestral allele within a population. Queller & Goodnight (1989) estimators of  $R$  for all dyads in the full study population of 253 individuals were calculated using the programme KINSHIP 1.3 (Goodnight & Queller 1999), and mean values were calculated for pairs of nearest-neighbour dominant males and dominant females.

When performing relatedness calculations using population allele frequencies obtained from the same data set as the individuals being measured, a bias correction must be

applied to those frequencies (Queller & Goodnight 1989). Individuals that are relatives of the individual(s) under consideration will tend to have allele frequencies closer to those individuals than the true population mean. Their inclusion in the limited sample of a data set thus biases the measure of population allele frequencies, resulting in an overestimation of baseline relatedness. To minimize bias when calculating  $R$ , members of the same cooperative group were coded as such, so that KINSHIP would disregard pairs of close relatives when calculating population allele frequencies (following Goodnight 2000). Our measure of baseline relatedness is likely to remain a slight overestimate, as short dispersal distances in the white-breasted thrasher mean that many individuals will have relatives in nearby groups. This was not considered to be a problem as it would tend to weaken our results rather than strengthen them.

## Results

### Dispersal

Of the 67 birds ringed as nestlings in 2002 and 2003, 33 were never resighted (14 males and 19 females), and 34 were resighted at least once in subsequent years. Most individuals that were resighted in their first year after fledging ( $n = 33$ ) had remained on their natal territory (73.3% of males,  $n = 15$ ; and 83.3% of females,  $n = 18$ ; Table 2). By contrast, almost all resighted birds had dispersed from their natal territory by the age of two (80% of males,  $n = 5$ ; and 100% of females,  $n = 3$ ; Table 2). Few birds were resighted 2 years after fledging, because access problems meant that the study area used in 2002 was different from that used in subsequent years. Females dispersed further than males (Table 2), although this difference was marginally nonsignificant ( $t = 2.01$ , d.f. = 12,  $P = 0.0675$ ).

Older birds did not often move territories. One female bird that was originally ringed as a helper was resighted breeding as part of an unassisted pair, having moved 220 m from the territory in which she was ringed (presumably her natal territory, since helpers are retained offspring). Only one dominant adult (again female) moved between territories in different years. Following the disappearance of her partner, she moved to an adjacent territory and settled with the resident male and his helper son. The previous female incumbent was unringed, and it is not known what happened to her. No adult males were recorded to move from one territory to another.

### Fine-scale genetic structure

Spatial autocorrelation analysis of the entire population of 98 adults whose breeding status and location during the

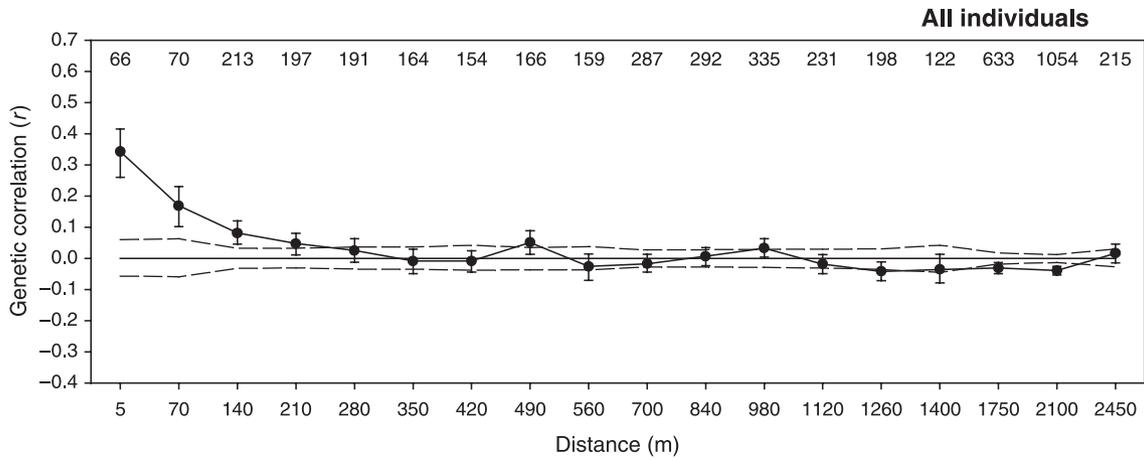
**Table 2** Proportion of resighted white-breasted thrashers that have dispersed from their natal territory categorized by age and sex, and mean distance traveled by birds that dispersed from their natal territory ( $\pm 1$  SE) categorized by sex

	Proportion of resighted birds that have dispersed 1 year after fledging	Proportion of resighted birds that have dispersed 2 years after fledging	Mean dispersal distance (m)
Males	26.7% ( $n = 15$ )	80% ( $n = 5$ )	103 $\pm$ 25.1 ( $n = 8$ )
Females	16.6% ( $n = 18$ )	100% ( $n = 3$ )	360 $\pm$ 145 ( $n = 6$ )

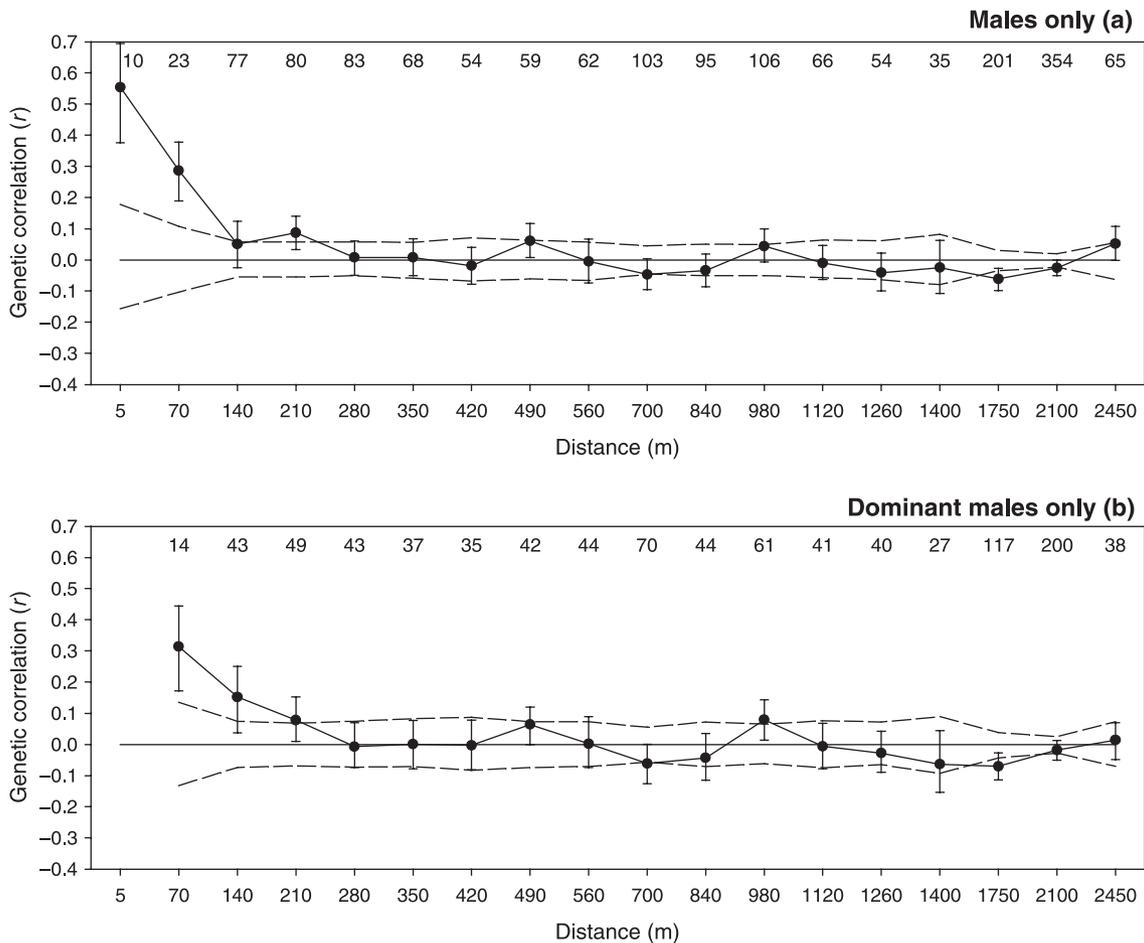
2004 breeding season was known showed significantly positive  $r$  values within the 5-, 70-, 140- and 210-m distance classes (Fig. 2). Near-identical results were found if the analysis was restricted to males, or to dominant males only (Fig. 3). The only difference was that, for males only, the  $r$  value for the 140-m distance class was significant only according to the permutational significance test, the more conservative bootstrapping method being marginally nonsignificant. On each territory, there was a single dominant male. In contrast, when restricted to females, or to female breeders only, the spatial autocorrelation analysis generally showed no significant relationship. For females only (Fig. 4), there was a strong positive autocorrelation within the smallest distance class ( $< 5$  m), consistent with dominant females sharing a territory with their helper daughters; there was only ever one dominant female per territory. There was also a weak positive correlation within the 140-m distance class, although when the analysis was restricted to dominant females only (Fig. 4) this effect was lost. The significant positive autocorrelation in the 280-m class does not fit the general pattern; it is worth noting that this distance class contained only six pairwise comparisons, the smallest sample size in the autocorrelation analysis. Male and female helpers were not analysed on their own because sample sizes were too small.

### Relatedness between nearest neighbours

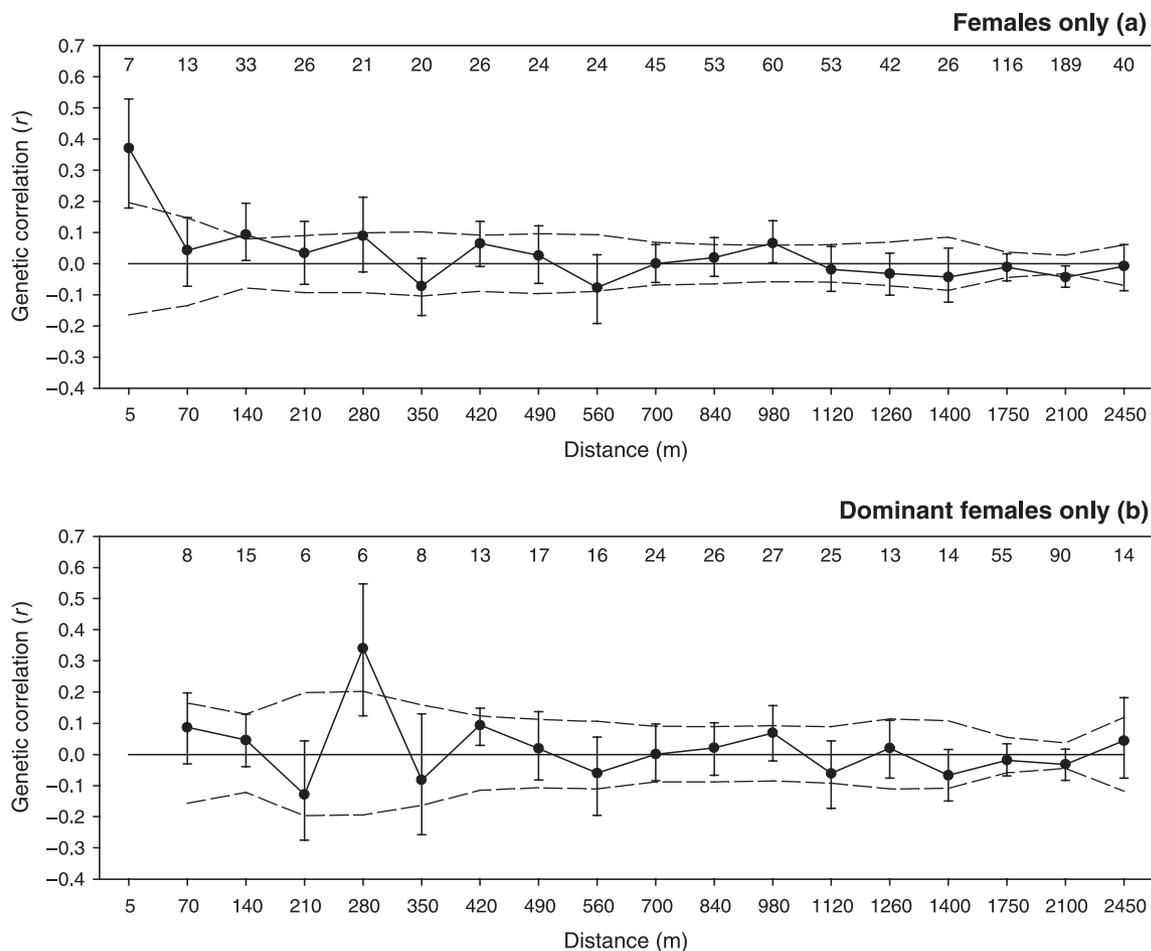
There was significant kinship (as measured by relatedness) between nearest-neighbour dominant males, but there was no such relationship between adjacent dominant females (see Fig. 5). The mean degree of relatedness between male neighbours was between that expected for cousins ( $R = 0.125$ ) and that expected between uncles and their nephews, grandfathers and their grandsons, or half-sibs ( $R = 0.25$ ). At  $0.191 \pm$  SE 0.063, the mean relatedness between nearest-neighbour dominant males was significantly greater than zero (the mean background relatedness between nonrelatives;  $t = 3.02$ , d.f. = 30,  $P = 0.005$ ), but not significantly different from 0.25 ( $t = -0.92$ , d.f. = 30,



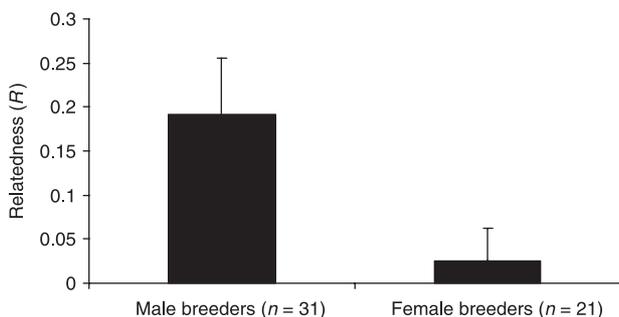
**Fig. 2** Correlogram plot of the genetic correlation coefficient ( $r$ ) as a function of distance for all individuals of known territorial status and location in 2004 ( $n = 98$ ). The permuted 95% confidence intervals (dashed lines) and bootstrapped 95% confidence error bars are also shown. The number of pairwise comparisons within each distance class is presented above the plotted values. Mean territory width was 70.0 m ( $\pm$  SE 5.76,  $n = 50$ ). All same-territory individuals were given identical coordinates and fall within the 5-m distance class.



**Fig. 3** Correlogram plots of the genetic correlation coefficient ( $r$ ) as a function of distance. The permuted 95% confidence intervals (dashed lines) and bootstrapped 95% confidence error bars are also shown. The number of pairwise comparisons within each distance class is presented above the plotted values. (a) Males only ( $n = 57$ ); (b) dominant males only ( $n = 44$ ). Mean territory width was 70.0 m ( $\pm$  SE 5.76,  $n = 50$ ). All same-territory individuals were given identical coordinates and fall within the 5-m distance class. Note that dominant males are on separate territories, so none falls within the 5-m distance class.



**Fig. 4** Correlogram plots of the genetic correlation coefficient ( $r$ ) as a function of distance. The permuted 95% confidence intervals (dashed lines) and bootstrapped 95% confidence error bars are also shown. The number of pairwise comparisons within each distance class is presented above the plotted values. (a) Females only ( $n = 41$ ); (b) dominant females only ( $n = 28$ ). Mean territory width was 70.0 m ( $\pm$  SE 5.76,  $n = 50$ ). All same-territory individuals were given identical coordinates and fall within the 5-m distance class. Note that dominant females are on separate territories, so none falls within the 5-m distance class.



**Fig. 5** Mean relatedness (Queller & Goodnight 1989) between nearest-neighbour dominant males and nearest-neighbour dominant females.

$P = 0.364$ ) or 0.125 ( $t = 1.05$ , d.f. = 30,  $P = 0.302$ ). Between neighbouring dominant females, the mean relatedness of  $0.025 \pm 0.038$  did not differ significantly from zero ( $t = 0.67$ , d.f. = 20,  $P = 0.510$ ).

## Discussion

Both genetic and observational measures of dispersal in the white-breasted thrasher showed that dispersal distances were sex-biased, with females dispersing over greater distances than males. This led to a marked fine-scale genetic substructuring of the male population, while no such effect was evident among females. The strength of the spatial autocorrelation was greater than that found in any previous study. Peakall *et al.* (2003) commented that it was noteworthy that the autocorrelation values ( $r$ ) they found for Australian bush rats *Rattus fuscipes* exceeded those typically reported for plants by more than four times, but the  $r$  values reported here are larger again (a maximum of 0.56 compared with Peakall *et al.*'s 0.3). The spatial autocorrelation technique used in this study has only once been applied to another bird species, the cooperatively breeding superb fairy-wren *Malurus cyaneus* (Double *et al.*

2005). Maximum autocorrelation values for the white-breasted thrasher were nearly three times greater than those reported for the superb fairy-wren ( $r = 0.56$  vs.  $r = 0.21$ ). This difference may well be related to the fact that extra-pair fertilizations are relatively uncommon in the white-breasted thrasher (Temple *et al.* in review), but account for more than 60% of offspring in the superb fairy-wren (Mulder *et al.* 1994; Dunn & Cockburn 1999; Double & Cockburn 2003). Since the majority of fertilizations in superb fairy-wrens are from dominant males three to four territories away from the breeding female, this militates against local genetic clustering (Double *et al.* 2005). High autocorrelation values may be expected in other cooperatively breeding species where helpers are philopatric offspring, rates of extra-pair paternity are low, and dispersal distances in one or both sexes are short, such as for example the laughing kookaburra *Dacelo novaguineae* or the bell miner *Manorina melanophrys* (Conrad *et al.* 1998; Legge & Cockburn 2000; Painter *et al.* 2000).

#### *Dispersal, kin clusters and cooperative breeding*

It has long been recognized that patterns of dispersal are related to the occurrence of cooperative breeding (Dickinson & Hatchwell 2004). Philopatric offspring of cooperative breeders (usually males) tend to breed nearer to their natal territory than do offspring of closely related species that are also year-round residents, but breed as pairs (Walters *et al.* 2004). Within facultative cooperatively breeding species, offspring that delay dispersal often acquire territories nearer to their natal territory than offspring that disperse at an early age (e.g. Austad & Rabenold 1986; Walters *et al.* 1988). On the basis of this difference, Zack (1990) proposed that delayed breeding and local dispersal were causally related, and hypothesized that philopatric individuals were staying home in order to queue for breeding vacancies on nearby high-quality territories. A central assumption of this hypothesis is that territory quality is spatially autocorrelated. If the turnover of breeding vacancies is slow, as is thought to be the case in many cooperative breeders, including the white-breasted thrasher (Temple *et al.* in review) for reasons related to both ecology and life history (Hatchwell & Komdeur 2000), there are numerous potential benefits of waiting on the natal territory while queuing for a local vacancy. The philopatric juvenile enjoys not only the benefits of remaining on a familiar territory (Ekman *et al.* 2004), but also, when the time comes to establish a territory of his own nearby, he may benefit from nepotistic assistance, or at least kin-selected tolerance.

Many birds show greater levels of aggression to non-relatives than to relatives. Male red grouse *Lagopus lagopus*

*scoticus*, for example, are more aggressive to nonkin than to kin (Watson *et al.* 1994), which suggests that, for young individuals attempting to establish territories, it is less costly for an individual to recruit within the immediate vicinity of a close relative (MacColl 1998). Pieltney *et al.* (1999) found that the majority of male grouse recruited into the adult population already had a first-order male relative established, supporting the hypothesis that recruitment is facilitated by behavioural interactions among relatives. White-breasted thrasher territorial males are, on average, as closely related to their nearest male neighbour as they would be to a nephew or grandson. This implies that establishing a territory by 'budding off' part of the natal territory to acquire peripheral parts of an adjacent territory may be easier in the white-breasted thrasher than in species where neighbouring males are not close relatives. Thus, a feedback loop may be created whereby short-distance dispersal by males leads to the formation of male kin clusters that facilitate nepotistic interactions and favour further local recruitment. This may lead to habitat 'supersaturation', an increase in the maximum population density caused by greater tolerance between conspecifics. The supersaturation hypothesis was proposed to explain the evolution of kin-based cooperative polygamy (Dickinson & Hatchwell 2004). They suggest that, if remaining on the natal territory reduces mortality, then the sex ratio will become biased in favour of the sex that stays home, and the availability of independent breeding vacancies will be constrained owing to a shortage of mates. The shortage of mates of one sex will mean that, for some birds of the opposite sex, sharing a mate may be the only way to achieve personal reproduction, and the best way to acquire that mate may be to wait on the natal territory and compete for breeding status there. Competition for space will be reduced through young birds associating with their natal groups, and consequently the population density will increase. Dickinson & Hatchwell's (2004) supersaturation hypothesis predicts, amongst other things, increased intergroup competition for space. The present study suggests, however, that there may be other routes to habitat supersaturation that do not require a polygamous mating system and that involve decreased rather than increased intergroup competition. In the case of the white-breasted thrasher, high levels of relatedness between adjacent territorial males imply that being a good neighbour may bring significant inclusive fitness benefits. Because rates of extra-group paternity are low (Temple *et al.* in review), males can also have high confidence in their relatedness to their neighbour's sons. Habitat supersaturation resulting from cooperative interactions within male kin clusters may be found in other cooperative breeders where independent breeding is constrained, male dispersal distances are short and extra-group paternity is low.

### Conservation implications

The rate at which animals disperse and the distances that they travel potentially have greater ramifications for conservation strategies than any other behavioural ecological variables (Caro 1998). Rates of dispersal between habitat patches influence population persistence (Durant 2000), gene flow between subgroups affects heterozygosity and genetic drift (Gilpin 1991), and the length that dispersers travel and their habitat preferences while travelling impact upon the design of protected area networks (Kooyman *et al.* 1996). However, with the exception of Population Viability Analyses (PVAs), there have been relatively few attempts to use empirical data on dispersal in conservation theory or practice (Caro 1998; but see Lidicker & Koenig 1996). For the white-breasted thrasher, the very short dispersal distances shown by males may have a negative impact on the species' ability to colonize new areas, even if habitat management or natural processes of succession did create new areas of suitable dry woodland or scrub. Additionally, the relatively short dispersal distances shown by both males and females may explain how it can be that the small northern subpopulation on St Lucia is apparently declining (Temple 2005), while demographic data from the southern subpopulation suggest that natality may currently exceed mortality in this area (Temple 2005). It is possible that, even though these two populations are only 6 km apart as the crow flies, this distance is too great for dispersing thrashers to cross readily. It would be interesting for a future study to sample both subpopulations and test for any difference in gene frequencies that might indicate reproductive isolation (Manel *et al.* 2003).

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